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THE FUNCTION, MECHANISM, AND EVOLUTION OF LEARNING AND BEHAVIOR: A REVIEW OF SARA J. SHETTLEWORTH'S COGNITION, EVOLUTION, AND BEHAVIOR

MICHAEL D. ZEILER

EMORY UNIVERSITY

Behavior is a property of living animals and is therefore a biological phenomenon. This book shows us what it looks like to have a truly biological science of behavior. Such a science needs to discover the laws that control behavior as it is occurring, and it is this that behavior analysts and other psychologists interested in animal behavior and learning have done so well. The science also needs to explain, however, the role that behavior plays in the life of the individual and in the existence of the species, and this has not been part of the agenda for most psychologists. Shettleworth addresses all of these questions about behavior. She views learning in terms of what it accomplishes for the individual and then provides insight into its causal laws and its evolution. All of this is accomplished with a critical eye and unremitting rigor. These accomplishments occur in the context of a theory based on a unique combination of domain-general and domain-specific processes that takes a major step in the direction of showing what students of animal behavior and animal learning have to offer each other.

Key words: learning, adaptive value, evolution, domain specificity, domain generality, behavior systems

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This book is a serious attempt to view behavior both in terms of its causes and what it accomplishes for the living animal. This combination is essential to put animal learning and behavior in a genuine biological context. It is also an outstanding example of what an evolutionary approach to psychology should be but never has been; a creative, scholarly, and intelligent synthesis of animal learning and animal behavior; and a manual on good methodology in the study of behavior. What it is not is a textbook of animal learning, comparative learning, or animal behavior, or any combination thereof. Each of these issues defines the rest of the review.

Cognition for Shettleworth refers to ''the mechanisms by which animals acquire, process, store, and act on information from the environment'' (p. 5). These mechanisms are the result of evolution. She takes issue with those who equate cognition with awareness, private states, intentions, and the like. Her approach to cognition is behavioral, but it does not exclude consciousness. Like B. F. Skinner, Shettleworth believes that private subjective states are real but not necessary for understanding adaptive behavior. Her reservations about consciousness seem to be tied to the difficulty of finding unambiguous ways to study it under appropriately rigorous conditions. Readers unhappy with explaining behavior by reference to evolved characteristics of the behaving organism might find this approach questionable, but then they might be uncomfortable with evolution itself.

Biological Explanation: The Four Whys

Chapter 1 of this book is required reading for anyone interested in behavior. One reason is that it contains what may be the best extant elucidation of Tinbergen's four whys of behavior. In his classic 1963 paper, Tinbergen described what it means for a biologist to understand fully why behavior is the way that it is. A complete explanation of any biological activity has four components, and all of these are not shared by explanations in the physical sciences. Tinbergen's view of biological explanation corresponds only in part to one borrowed from Newtonian physics.

One of the whys of behavior is the explanation of what triggers the behavior right now. What current environmental or physiological events or processes elicit or control the behavior? Another why is developmental, with development broadly construed as history. What previous experiences and genetic

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Address reprint requests to the author at the Department of Psychology, Emory University, Atlanta, Georgia 30322 (e-mail: psymdz@emory.edu).

mechanisms are responsible for the behavior occurring now? The third why is what the behavior accomplishes for the animal. Tinbergen (1963) phrased this as the survival value of the behavior. Shettleworth construes it more broadly as the function of the behavior, with function defined in terms of adaptive significance for the individual animal. The fourth why is how some particular behavior evolved within and across species. The four whys of behavior, then, are causation, development, function, and evolution. In short, Tinbergen emphasized that a full biological explanation of any behavior must explicate the laws leading to and maintaining the behavior (causation and development), describe the role that the behavior plays in the survival of the individual (survival value), and show how the behavior influences reproductive success and thereby continues or not across different species (evolution). A true and complete biological explanation, then, demands attention to the antecedent causes of a behavior pattern, its consequent effects on the well-being of the animal, and its long-term effects on the species. Answers to all of the four whys constitute the complete biological explanation for any behavior and provide the foundation of Shettleworth's integration of animal learning and animal behavior.

Psychologists who have studied animal learning have emphasized causation, whereas ethologists have cared more about function and evolution. Another way of saying this is that psychologists asked about the immediate and preceding historical events responsible for the behavior (*proximate explanations*), whereas ethologists asked about its future effects on the individual and the species (the immediate and long-term *ultimate explanations*). The reason that psychologists have tended to ignore function and evolution is attributable to the use of Newtonian physics as the model of proper science. This view prevailed at the time that psychology emerged from philosophy as an independent discipline. From that perspective, good science concentrates on the immediate antecedent events that produce a phenomenon, for example, some kind of behavior. A proper science shuns attempts to explain why such causal laws exist, and only engineers care about utility.

A science of life processes could not be happy with this model. For biology, a phenomenon, be it anatomical, physiological, or behavioral, is interesting only because it has a role in sustaining life. So, a biological perspective means not only understanding the factors that produce some behavior but also knowing how the behavior affects the well-being of the individual. And that is not all. Darwinian evolutionary theory asks why the causal laws are as they are. It emphasizes the importance of knowing how evolved processes and causal laws relate to the development, maintenance, or extinction of a species.

Unfortunately, it is easy to confuse ultimate outcomes with proximate causes. Examples of this characterize such arguments as whether behavior is determined by local events or is optimal with respect to maximizing reinforcement frequency, or whether avoidance is the product of contiguity or reduction in the frequency of aversive stimuli. I wonder whether the theoretical conflicts between molecular versus molar explanations of behavior are not the result of failing to distinguish between looking back in time to describe the immediate events that cause the behavior (causation) and looking ahead in time to describe what the behavior accomplishes (its function for the animal). The events that trigger some behavior should not be confused with what that behavior accomplishes.

Causation and function always should have been recognized as complementary. Although their equal validity might seem obvious now, this was not the case historically because psychologists and biologists treated behavior differently. Psychologists studied behavior to analyze processes presumed to be general within and across species, whereas biologists were interested in the behavior patterns themselves. The general process view, which fits well within the physical sciences, had its main base in North America where the primary emphasis was on animal learning. The biological view developed mainly in Europe and cared about the behavior of some particular species living in its normal environment. Experimental psychologists studied animals in the laboratory in the effort to discover basic and general learning processes. Ethologists studied animals in the wild in the attempt to understand some specialized form of behavior like foraging, or homing, or hibernation. Psychologists studied behavior like bar pressing or key pecking by rats and pigeons, which had no obvious counterpart in the behavior patterns characteristic of these species when living outside the laboratory, to elucidate the general rules of causation and development. It would hardly make sense to care about the adaptive value or the evolutionary basis of responses invented for use in the laboratory. Evolution entered the picture for psychologists in the assumption that the processes being analyzed had universal generality across species and were independent of the particular responses and stimuli chosen for study, just as laws of falling bodies are independent of the bodies that fall. If processes are indeed fully general, the appropriate criteria for choosing stimuli, responses, and experimental species are convenience, efficiency, and the ability to build on existing data.

Biologists, however, were studying what wild animals actually do in their natural environments. The highly stereotyped forms that these behavior patterns took and their generality across all members of the species suggested that they were not arbitrary but were the products of evolutionary forces. The behavior patterns themselves were what captured attention. The big picture that integrated the study of specialized and clearly important types of animal behavior was evolutionary theory, which established generality or diversity through comparative analyses of how the behavior influenced reproductive success among the different species. Process analysis was largely restricted to analyzing the stimuli that released the evolved behavior patterns. This was very different from the general process approach taken by psychologists, who discovered laws through manipulating convenient responses and stimuli rather than by dealing directly with behavior important to survival in the animal's natural environment. It may not be surprising, therefore, that psychologists and biological animal behaviorists could see each other as largely irrelevant.

Shettleworth would certainly agree with experimental psychologists were they to say that something like a full biological explanation of behavior is achievable as long as all four of Tinbergen's (1963) whys are answered rigorously. These experimentalists might add that we know how to be rigorous about causation and development and maybe even about the consequences of some behavior for the animal, but what we have seen in the case of analyzing evolutionary function is not impressive in this regard. Most of it seems to be little more than exercises in historical storytelling.

Shettleworth answers this concern by describing relatively recent advances in methods for testing evolutionary explanations. Her question is: "On what method for testing adaptation is this argument based, and how rigorously was that method applied?" (p. 33). The problem is that standard experimental procedures cannot be used to study the evolution of any species, and the necessary historical data are unavailable to document the evolution of any pattern of behavior. The presumed independent variables cannot be manipulated, generational time is too long (except for bacteria or viruses that reproduce with alarming frequency but are not likely to show much interesting behavior), and behavior leaves no fossils.

It is possible to determine what some behavior pattern accomplishes in its present form. If the behavior has current adaptive value, that adds plausibility to the argument that the behavior was adaptive in the past and thereby would have evolved. Shettleworth uses as an example Tinbergen's (1963) research on eggshell removal by gulls. Gulls remove empty eggshells from the nest soon after the chicks hatch. In experiments designed to determine the consequences of leaving broken eggshells near the nest, it was found that removing the shells reduced predation. These data on current function add credibility to the hypothesis that eggshell removal evolved through natural selection. Eggshell removal, like vertebrate eyes or parental behavior, works so well in promoting survival and reproductive success that it could not have arisen and been maintained over numerous generations by chance alone. Of course, contemporary function is not proof of evolutionary function, but it does add a measure of confidence to the evolution-by-natural-selection hypothesis.

An initially appealing technique for establishing an evolutionary scenario stemmed from the idea that prolonged natural selection would create ideally adapted behavior patterns. What distinguished this argument from one based on religion or on pure storytelling was the quantification of ideal design by the use of formal optimal foraging models (see Stephens & Krebs, 1986, for a detailed review of the logic of the theory and much data). The strategy is to develop equations that describe the behavior that would occur if a particular evolutionarily important function (e.g., energy conservation) were accomplished perfectly. This, then, is compared with the actually observed behavior. If the correspondence between prediction and reality is perfect, it supports the idea that the behavior evolved to serve that function. Unfortunately, the correspondence has usually been substantially inexact, whether the behavior analyzed has been whelk dropping by crows, copulation time by dung flies, or anything else (cf. Kitcher, 1985). When discrepancies have been excused by invoking constraints (inadequate physiology, the need to deal with other problems at the same time, etc.), they have amounted to little more than common sense grafted onto the fervent belief that evolution works perfectly to generate ideally adaptive behavior. This then requires ever more complicated equations, but evolutionary theories that recognize the importance of processes other than natural selection are far more difficult to manipulate in any very quantitative manner. It is not hard to understand why enthusiasm for this method of analyzing evolution might dim. In my view, which in hindsight is quite nicely supported by the unsatisfactory fits between theoretical and actual behavior, the problem is that perfect design achieved through natural selection was an ill-founded concept to begin with. I will return to this issue in the next section on evolutionary psychology.

A stronger way of testing evolutionary explanations is the comparative method. The beauty of the comparative method is that it is based on rigorous comparisons across different species. The idea is to relate the degree to which animals that do or do not share a common behavioral trait do or do not share common selection pressures. For example, kittiwakes, gulls that are not subject to predators because they live in cliffs, do not remove broken eggshells from the area of their nests. Shettleworth explains in some detail how vulnerability to predators, the seasonable availability of high-quality food, body size, and other physical traits and environmental factors successfully account for similar patterns of social organization in ungulates, birds, and primates.

This useful introduction to methodology is instructive for those who think that any of Tinbergen's (1963) whys other than causation and development boil down to nothing better than exercises in the literary creativity involved in the construction of plausible and engaging just-so stories. A proper biological science of behavior must rigorously describe the short- and long-term outcomes of behavior and the factors that trigger and control the behavior at the moment it is occurring. We cannot understand behavior without knowledge of both causation and function.

Evolutionary Psychology

The contemporary reader may jump to the conclusion that this book promotes evolutionary psychology. Evolutionary psychology claims to offer a coherent evolution-based theoretical framework for understanding all psychological phenomena. Shettleworth is sympathetic to evolutionary psychology, but she is concerned about its lack of rigor. What she does not explain is that evolutionary psychology is also not rigorous in its connection to the best of contemporary evolutionary theory. I would like to point out here why a central principle of evolutionary psychology—that psychological processes must in principle be domain specific rather than domain general—does not follow inevitably from evolutionary theory. I do so because it is important to distinguish the domain specificity of evolutionary psychology from the novel and exciting form of domain specificity that lies at the heart of this book.

Evolutionary psychology is sociobiology renamed (Konner, 2002). This means that evolution is viewed almost exclusively in terms of Darwinian natural selection. This is known as *adaptationism* in the evolution community. No student of evolution disputes that natural selection is important, but the more comprehensive view (see Ridley, 1997) is that it is one of many processes responsible for evolution. Only a radical subgroup would claim that natural selection is the sole source of evolutionary change, and even they are likely to at least pay lip service to these other processes before going on to ignore them.

Of particular importance is the question of what generates the variations that natural selection works on. For the arch adaptationist, cumulative natural selection not only chooses among variations but also is responsible for generating most of the variations. Changes occur because selection moves the distribution of phenotypic characteristics by favoring extremes (directional selection), whereas stability occurs because selection favors the existing distribution (stabilizing selection). Directional selection, however, is not the only possible scenario for change. Other processes may generate variations (mutation, genetic drift, environmental changes, and many others as well), and natural selection may serve mainly to screen the changes rather than to serve as their primary creator. The distinction is important, because it shifts emphasis from directional natural selection that operates inexorably to generate characteristics that ever more efficiently maximize fitness to natural selection as a process that operates mainly to review the acceptability of what has been generated in other ways. For adaptationists, directional natural selection, operating over enough generations, must inevitably result in behavior patterns that perfectly maximize fitness. If, however, variations come from other sources, natural selection guarantees only that a feature is good enough to allow some minimal level of reproductive success. Existing behavior patterns need not be optimal; they must only be good enough.

These disparate views result in important differences in applying evolutionary concepts to behavior. From the adaptationist perspective of evolutionary psychology, general process theories of behavior cannot possibly be true. The same learning strategies could not apply to all learning situations, because they would not provide the best possible solution to each enduring challenge that animals face. For example, how animals learn about food could not possibly be the same as how they learn about danger, because different learning strategies would be more effective in the two cases. Indeed, learning about one kind of food would not pertain to another, if different strategies would work better for each. Also, the processes cannot be the same for all species, because each has its own ecology. How a generalist feeder like the rat learns about food sources cannot possibly be the same as how more specialized feeders learn about food. For the arch adaptationist, behavioral processes must be domain specific rather than domain general.

The flaw in this premise is that evolutionary processes entail no commitment to perfection. Even though a given strategy may not be ideal in solving all survival problems, it still may prevail if no better alternative ever appeared to be selected. And here is where Shettleworth proves not to be an evolutionary psychologist. For example, she believes in the domain generality of associative learning in solving certain kinds of problems in learning about causal relations, even though one could imagine that the learning of different kinds of causal relations might be served better were they more specific to particular tasks. To quote her directly:

> Behavior is not usually governed by a representation of the optimum as such but rather is the outcome of various simple mechanisms that have presumably been selected because in nature they lead to outcomes fairly close to the optimum most of the time. (Shettleworth, 1998, p. 486)

Also, as we will see, she argues persuasively for the possibility of other general processes as well, although she creatively embeds them in the context of domain specificity.

Many of us are enthusiastic about the possibility of evolutionary biology providing a powerful foundation for integrating all of psychology. But that promise is not met by the kind of simple-minded adaptationism that has already proven to be a failure in the guise of sociobiology. Evolutionary psychology is doomed to be a fad, just as was the case for sociobiology. I am very pleased, therefore, that Shettleworth really has not jumped on that bandwagon. However she might feel about mainstream evolutionary psychology as it is at this time, and no matter how happy evolutionary psychologists might be to have her in their camp, her approach to evolution and behavior as represented in this book simply does not fit the pattern.

Domain Specificity and Generality: Behavior Systems Theory and Belongingness

All of us know about instinctive drift, taste aversion learning, and the other kinds of phenomena that have led to the conclusion that behavior is replete with adaptive specializations. That we now have a theory that renders these so-called anomalies not anomalous is less widely recognized. Timberlake (1983) brought behavior systems theory into modern behavior theory. This theory is an ecological-evolutionary guide to understanding the kinds of learning that are favored or discouraged by particular situations. It explains all of the apparent anomalies and adaptive specializations and even predicts others. Shettleworth has played a significant role in the development of behavior systems theory with her work on food caching by different species of birds.

The foundation of behavior systems theory is the concept that animals confronted by new situations bring with them preexisting tendencies as products of evolution to treat events in certain ways. Not all species do the same thing when they encounter signals for food, and they also show characteristic responses when confronted by signals for danger or when solving any of the other problems that arise in their lives. The signals and responses for food or danger or mating or other crucial events usually are not the same. Shettleworth uses the term *belongingness* to refer to the kinds of responses those members of the species display when confronted with particular salient events in nature and the stimuli that usually predict them. Animals can learn about other signals, and they can be taught to develop different kinds of behavior, but preexisting biological significance has important effects on how readily they will learn.

This is different from saying that the failure of learning to occur equally well with all stimuli, responses, and reinforcers must mean that laws of learning are not general. It means that animals are not blank slates when they enter the laboratory, but instead bring with them well-established tendencies that have developed during the evolution of their species. One can predict their initial behavior in the laboratory from knowing what they do in their natural environment. Saying that learning is affected by the particular stimuli, responses, and reinforcers involved is quite different from saying that they learn by different processes when they do learn. What have been called biological constraints on learning have all referred to what animals can and cannot learn readily, and all of these are explained by behavior systems theory. It will become evident in the next section that Shettleworth goes a step further by proposing that multiple learning processes have evolved to deal with the different kinds of problems that animals face in nature. Learning is not a unitary process but instead is itself a set of adaptive specializations.

Domain Specificity: A New Look at Learning Processes

Learning theory has never been dominated by the idea that all learning is the outcome of identical processes. For example, it would hardly seem either revolutionary or noteworthy to propose that operant and Pavlovian conditioning are different. Shettleworth's organizational approach to differentiating types of learning is unique, however. She approaches the issue of process generality from the perspective of how learning allows animals of different species to cope with the problems that they confront now and that presumably have persisted over evolutionary time. The underlying hypothesis is that learning processes may be general for each type of learning. For her, then, domain specificity refers to particular types of learning differentiated by the functions they serve. Within each functionally defined domain, however, the underlying hypothesis is that learning may follow the same causal laws.

Chapter 2 is not about learning, but it sets the stage for what is to come. Although it is about the need for animals of all species to discriminate among the wealth of stimuli existing in their environments, it illustrates the point that what looks like adaptive specialization actually reflects common causal properties. Animals need to discriminate stimuli in order to find food, or mates, or to avoid predators, or to identify their offspring. All do not have the same sensory physiology, and so all do not respond to the same environmental events. Naturalistic observations of behavior as well as more focused data from behavioral ecology reveal that some species see colors and others do not. Bats are sensitive to ultrasonic energy and bees to ultraviolet light and pigeons have two foveae in each eye, but most other species do not. All of these differences and similarities in sensory ability can be understood in terms of the ecological niche occupied by each species, just as is the case for adaptive specializations in learning.

Despite their differences in the underlying physiology of their sensory systems, all species that have been studied have demonstrated the same psychophysical principles such as Weber's law, increased behavior to stronger stimuli, habituation, contrast effects relative to background stimulation, and the like. In addition, all behave as predicted by signal detection theory, and all animals studied, independent of their preferred sensory modality, reveal similar principles of selective attention to stimuli. Apparently, perception displays substantial generality despite differences in species and stimulus modality. Common function—the need to discriminate stimuli—seems to be correlated with common causation.

Chapter 3 moves on to learning. Shettleworth proposes that associative learning evolved to serve the function of learning about physical causal relations, a need that most if not all species share. Associative learning (Pavlovian conditioning) is the learning responsible for establishing causal relations, but it is not equally effective with all stimuli, because effectiveness derives from the belongingness of events. So, the laws of associative learning may not describe all learning, but they do provide a general process account of one kind of learning. After describing the need for appropriate control conditions when analyzing associative learning in different species and explaining basic phenomena like blocking, contingency, and inhibition, Shettleworth goes on to describe the utility of the Rescorla–Wagner model. Although the model integrates much data of Pavlovian conditioning, its failure to allow for belongingness limits its generality. The Rescorla–Wagner model does illustrate that associations developed through simple contiguity enable animals to track causal relations without their having any actual representation of causality.

The subsequent chapters follow a similar pattern, each addressing a different function served by learning. Chapter 4 is concerned with the need to learn about single events, chapter 5 with the need to discriminate among stimulus inputs, chapter 6 with the importance of retaining information, chapter 7 with the universal need to orient in space, chapter 8 with timing and counting, chapter 9 with foraging, and chapter 10 with the need to learn from others. All begin with the function of solving these problems in the natural environment and are replete with references to both field and laboratory studies. Each of the learning problems treated may involve its own principles (domain specificity), but each type may follow general rules (generality within the domain). Domain specificity is found in process, not content.

A General Process Theory of Learning About Single Events

Chapter 4 offers such creative and exciting insights that it warrants special mention. Its focus is on the need for animals to learn about single events. Shettleworth refers to this as *simple recognition learning,* because the stimuli have no obvious relation to other events. To my knowledge, this is the first time that habituation, perceptual learning, imprinting, and kin recognition have been grouped together as instances of one type of learning, despite the different functions that each accomplishes. What we have is a hierarchy of functions, with the top level defined by the need to recognize single events and the next level being what the particular type of recognition accomplishes. The causal laws basically are general for all types of simple recognition learning with some modification by its specific form.

Habituation has enormous generality across species, having been seen at all phylogenetic levels including single-celled organisms. Continued exposure to the same stimulus results in changes in responding. The function of habituation seems to be learning to ignore events that have no consequences. After reviewing the standard controlling variables like number of stimulus presentations, stimulus intensity, spacing of presentations, and the disruptive effects of sensitization, attention shifts to a discussion of habituation theories.

Perceptual learning refers to learning the characteristics of individual stimuli and not about their relations to other events. For example, when rats are exposed to a stimulus, subsequent tests in which the stimuli do predict something show that they had learned its properties. It is not obvious to me whether perceptual learning qualifies as a different category of simple recognition learning or is more properly viewed as a by-product of habituation. It is further proof that stimulus properties are being learned even when the animals are learning to ignore the stimulus during habituation. This brief section might have included some discussion of Lashley and Wade's (1946) theory of how animals come to discriminate the properties of stimuli. The importance of that theory lies in its suggestion that initial exposure to a stimulus will not automatically produce learning of all of its attributes or of any at all in the absence of a history that teaches the animal that the stimulus is relevant to something. Habituation training actually may be doing that by teaching that the stimulus currently is irrelevant.

Imprinting commands a lot of attention, not because, as once thought, it uniquely demonstrates genetic determination of a particular type of learning, but because it deals with interesting phenomena. From Shettleworth's perspective imprinting is no more genetically preprogrammed than is any other kind of learning. All types of learning are genetically preprogrammed. They differ in the content of the preprogramming, not in its presence or absence.

Birds imprint to a stimulus from mere exposure to it, thereby making it a form of simple recognition learning. One form of imprinting, *filial imprinting,* refers to young birds becoming attached to their mother or other stimuli that they have been exposed to early in life. Another form, *sexual imprinting,* refers to mate choices based on these early experiences. These preferences are normally for members of the birds' own species, but early exposure can result in preferences for inanimate objects or for members of a different species. In a famous case, a bird that imprinted on Konrad Lorenz courted him in favor of a member of its own species when it reached sexual maturity! As it is unlikely that sexual activity with a member of a different species can result in reproductive success, having to learn one's species seems to be a less than optimal mating strategy. Should it require learning to pick mates slightly different from one's mother or siblings in order to minimize inbreeding?

Shettleworth does not ask why learning should be implicated at all in a system in which reproductive success allows no errors, but she does discuss the possibility that sexual imprinting is a mechanism for controlling inbreeding and outbreeding. Data she presents indicate that filial imprinting occurs when birds are very young, but sexual imprinting occurs when birds are still in the family group but are starting to develop adult plumage. The object of filial imprinting, then, seems to be the mother, but the objects of sexual imprinting may be mainly the other animals that live in close contact. But there is more to it than simply being sexually attracted to the most familiar individuals, because familiarity seems to breed some element of contempt. When sexually mature quail were housed with cousins, they laid fertile eggs sooner than if they were housed with siblings. These data suggest that sexual imprinting produces preferences that operate against close inbreeding while facilitating outbreeding with other members of the species. Shettleworth concludes, "there is little evidence that too much outbreeding is a bad thing as long as matings between species are avoided. If this is so, preferences for close but not-too-close relatives may function only to avoid too much inbreeding" (p. 167).

A dissociation of filial and sexual imprinting is an attractive idea. Many species seem to share the characteristics of sexual imprinting in arriving at preferences for mates, but the details of filial imprinting seem to be mainly confined to certain species of birds. Of course, this still does not explain why such preferences need to be learned and can lead to a bird being sexually attracted to Konrad Lorenz. Once again optimality theory falls short of reality. Perhaps the answer is that the optimal genetic mechanisms for generating hardwired preferences for distantly or unrelated members of the same species never existed to be selected, and learning through imprinting was the best that natural selection could do.

A dominating influence on research in filial imprinting was Lorenz's early conclusion that the learning occurs only in a relatively brief early period of maximal sensitivity and that it is irreversible once it develops. These characteristics might seem to differentiate imprinting from other kinds of learning. Shettleworth points out, however, that the utility of a baby imprinting on its mother and staying away from other adults who might attack it is restricted to early life. That imprinting is useful only for babies does not mean that imprinting is fundamentally different from other kinds of learning, because these too occur only under certain conditions. More critical is the claimed irreversibility of imprinting, because most other kinds of learning are reversible. Imprinting appears to be reversible only if the initial object was artificial.

As I thought about Shettleworth's discussion, it struck me that Hoffman's (1996) data on the sensitive period and reversibility might suggest another parallel between forms of single stimulus learning. Hoffman found that both the critical period and irreversibility seem to be the product of the development of neophobia, that is, the point in development at which young animals become fearful of any new stimulus. Infants are not afraid of novel objects at birth; they develop this fear later in life at a time that approximates the end of the period of maximal sensitivity. Young birds will imprint on a novel object after the critical period has ended if exposure to it is maintained; they will reverse their imprinting from an established object to a new one if the old is withdrawn and the new is maintained. Is this in some way similar to sensitization, in which habituation is lost to a familiar stimulus when a sudden strong novel stimulus appears? Habituation to this new stimulus occurs only when the initial emotional response to it dissipates. Is this showing that neophobia also plays an important role in habituation?

As if integrating habituation, perceptual learning, and imprinting into one type of learning was not enough, Shettleworth includes the phenomenon that once provided the single biggest challenge to an evolutionary explanation of behavior. That puzzle was why animals sometimes do things that enhance the fitness of others while hurting their own. The solution led to a fundamental change in the conception of fitness. Hamilton (1963) recognized that helping others reproduce actually would have an evolutionary benefit for the altruist if the sacrificial acts were confined to relatives. The concept of *inclusive fitness* is that reproductive success should be measured in terms of the survival of the individual's genes, regardless of whether they came from that individual or from those who share the same genes. Inclusive fitness explains not only helping others but also the evolution of sterile worker castes of insects. Those that never themselves reproduce benefit the future gene pool by helping their close relatives care for their offspring. The concept of inclusive fitness was emphasized in sociobiology, and it now is one of the pillars of evolutionary theory. Note that the behavior is only superficially altruistic; it really occurs only because it confers advantages on the so-called altruist, or more precisely, the altruist's genes. The concept can be expanded to include unrelated animals, if altruistic acts toward them are reciprocated and thereby contribute to long-term advantages. This is known as reciprocal altruism. All forms of altruism, then, share the property of occurring only because they promote survival of the altruist's genes.

If animals are to be altruistic only toward their relatives or toward those who will reciprocate, they must be able to discriminate their kin and potential returners-of-favors from others. This discrimination underlies the concepts of kin recognition and kin selection. Shettleworth provides a thoughtful discussion and analysis of whether behavior really does favor kin. This is not an easy area to study either in the laboratory or in the field. Virtually all of the data can be explained in other ways (e.g., being nice to all of those who lived in the nest with you could explain altruism directed at relatives just as imprinting illustrates the rule that the first large moving object encountered in your environment is to be treated as your mother). Exemplified here is Shettleworth's typically thorough and original treatment of problems that most evolutionary psychologists take for granted. And she adds the new twist of seeing kin selection as one more case of simple recognition learning.

No mention is made of another general process that may be the causal mechanism for many forms of altruism. Simon (1990) proposed a proximate mechanism for altruism that has nothing directly to do with benefits to the altruist. This argument does not challenge the idea that inclusive fitness is the ultimate explanation, but it does remove the need to believe that altruism itself is genetically based. If animals have evolved to learn from others because that has improved inclusive fitness, they can be altruistic without being self-serving. That animals do indeed learn many different things from others is amply documented in chapter 10. Simon's argument is human oriented, but it need not be confined to our species. ''Fitness can be enhanced by . . . [training] . . . that induces individuals often to adopt culturally transmitted behaviors without independent evaluation of their contribution to personal fitness'' (Simon, 1990, p. 1665).

This is not to gainsay the importance of learning whom to learn from and whom to favor and whom to ignore. These processes are eminently attributable to a history of differential reinforcement operating through the genetically established tendency to interact with and to learn from others. Altruism is the outcome of learning processes that have been established through their effects on inclusive fitness rather than through a gene promoting self-sacrifice.

Filling in the Gaps: What It Is and What It Is Not

The body of this review emphasized biological explanation, evolutionary psychology, the creative contributions of the book, and Shettleworth's synthesis of learning and animal behavior. No more need be said about those features. What about the value of this book as a textbook for courses in learning?

It is not a conventional textbook. The typical learning textbook describes the rules underlying each relevant process being considered. Shettleworth's book does so as well, but not in a way that teaches students many of the basic principles of animal learning. It covers a number of the various processes and methodological issues of Pavlovian conditioning, but it largely ignores numerous basic phenomena of operant behavior. It does describe what is known about learning processes that can be related to functionally important problems of survival. The teacher of a course in operant behavior might be gratified by the inclusion of the relevance of the matching law and open and closed economies to foraging, but might be puzzled by the absence of simple schedules of reinforcement or conditioned reinforcement or principles of shaping or avoidance or punishment or even the parallels between natural selection and operant reinforcement. The typical textbook on behavioral ecology or animal behavior tends to deal with the problems animals face in nature and the adaptive significance of the various behavior patterns that have evolved because they promote survival and reproductive success. The teacher of such a course will find that Shettleworth's book is as selective in this regard as it is in animal learning. This book is more likely to serve as an inspiration and source for lectures than as an undergraduate class textbook. The book is a natural for use in a graduate seminar, however.

Students would benefit greatly from being exposed to a book so committed to rigor. Shettleworth has an enormous talent for deflating conclusions based on inadequate data and shoddy thinking. This is strikingly manifest in chapters 11 and 12, in which she provides penetrating methodological and conceptual critiques of contemporary cognitive ethology with its emphasis on self-recognition, intentionality, and animal communication. Cognitive ethology differs from both classical ethology and behavior analysis by explaining behavior in terms of mental states.

> Most classical ethology is very behavioristic, in some ways not so different from Skinnerian psychology. . . . But in classical ethology, in contrast to Skinnerian psychology, describing behavior was just the beginning of an analysis of internal causal organization, function, evolution, or development. (pp. 476–477)

In contrast, cognitive ethology attributes behavior to an animal's internal subjective experiences.

Has cognitive ethology worked? Shettleworth provides the following example. While a plover is sitting on eggs, a fox appears. The plover moves away from the nest, dragging its wing, until the fox follows it far from the nest. Then the plover abandons its fake injury and flies straight back to the nest. Did the plover have the conscious intention of deceiving the fox? Was its behavior guided by this intention? Cognitive ethologists assert that the goal directedness of such behavior is unambiguous evidence for the control of behavior by consciousness. Shettleworth is not impressed with their attempts to prove their belief. After all, control systems like thermostats achieve goals with no mental representations. Wood lice move about randomly until they find a damp dark locale and then stay there. Does this mean they have a conscious representation of what they want? Until proper experiments are done to investigate whether or not the plover's behavior is a reflexive response to subtle releasing stimuli, the interpretation as intentionality is premature. When a chimpanzee recognizes itself in a mirror, does it mean that it has a theory that it and others have minds? No good evidence exists for such a concept. What about the primates or other animals that show no sign of behaving as if it is themselves reflected in the mirror? Shettleworth provides numerous additional claims for animal cognitive awareness, and deflates them all. None of the evidence meets minimal standards for rigor. So, although not a conventional textbook, the book is a guide to proper thinking in the scientific study of behavior.

Shettleworth has provided students of both learning and animal behavior with a new and unremittingly rigorous way of looking at their field. She has shown us what evolution and ecology have to offer the scientific study of learning and what animal learning has to offer behavioral biology. She shows why learning is a crucial process in the maintenance of life. This book is essential reading for any contemporary student of behavior.

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